With Compliments of D. Folsom

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POTATO SPINDLE-TUBER

CONTENTS

MAINE

AGRICULTURAL EXPERIMENT STATION

ORONO, MAINE

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BULLETIN 312[1]

POTATO SPINDLE-TUBER.[2]

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SUMMARY

(1) Poor shape of potato tubers is brought about by soil conditions, weather conditions, diseases, and unknown causes.

(2) One important cause of poor tuber shape and of potato degeneration or running-out is a disease called spindle-tuber.

(3) The effects of this disease upon the vines and tubers are generally alike in different varieties, but not exactly so. These effects are described.

(4) Spindle-tuber is perpetuated in the tubers and other juice-containing parts of the plant, without showing any effects

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[1]This bulletin is intended to make available to Maine potato growers certain facts disclosed by investigations conducted as a cooperative project by the Department of Plant Pathology of the Maine Agricultural Experiment Station and the Office of Cotton, Truck, and Forage Crop Disease Investigations of the Bureau of Plant Industry. Many of these facts have been given in other publications, namely, Schultz, Eugene S., and Folsom, Donald. A "spindling-tuber disease" of Irish potatoes. Science n. s. 57:149. 1923.————Spindling-tuber and other degeneration diseases of Irish potatoes. (Abst.) Phytopath. 13:40. 1923.————Transmission, variation, and control of certain degeneration diseases of Irish potatoes. Jour. Agri. Research, Vol. 25, No. 2.

[2]In choosing a name for the earlier papers, the writers seriously considered the term "spindle-tuber disease" and would have used it instead of the name "spindling-tuber disease" had they known of its practical use in New Jersey as described by Wm. H. Martin ("Spindle tuber," a new potato trouble. Hints to Potato Growers, New Jersey State Potato Assocn., Vol. 3, No. 8, December, 1922. Reprinted in the Aroostook County Farm Bureau News, Vol. 4, No. 3, February, 1923.) While there is too much similarity between the two terms to allow the matter to become very important, it is thought preferable to adopt the New Jersey name altogether; it not only has been put to practical use by the New Jersey growers, but also refers to the characteristic tapering of the ends of the tubers, and is not so easily confused with the term "spindling-sprout."

until more or less time has elapsed after the original introduction of the cause of the disease.

(5) Spindle-tuber spreads from diseased to healthy plants. It has been transmitted thus by aphids (plantlice) and by certain artificial methods of juice-transfer.

(6) Further study may show that this disease, like other degeneration diseases, is affected by conditions of weather and climate in regard to its effects on the plants and in regard to its rate of spread.

(7) The securing and isolation of disease-free stocks seem more advisable as control measures than tuber selection, hill selection, removal of diseased hills, and attempts at insect elimination. Disease-free stocks are available but they usually have not been planted in isolation, so that only a few practical tests of isolation have been observed.

CAUSES OF POOR TUBER SHAPE

It is well known that tuber shape may vary considerably within a variety of potatoes even in the same field, and that the general or average shape of the tubers cut for seed often is not resembled closely by the shape of the tubers dug at the harvest. Differences in average tuber shape observed in different parts of a field have been attributed to soil differences. For example, the writer of this bulletin has seen the same seed stock planted on low, dark soil (Washburn loam) and on high light soil (Caribou loam) with darker color and more gnarled, poor-shaped tubers appearing in the crop from the low soil, especially when it was too wet for part of the season and was baked hard the last part. This was true for several varieties in several localities in 1922 in northeastern Maine. Thus it is seen to be possible for soil conditions to have a direct effect upon tuber shape.

Change in the average tuber shape from season to season, or from seed stock to the dug crop, in a given strain or stock, has been attributed to differences in soil, weather, or both. It is clear why good-shaped stock grown one year on good soil might, if planted the next year on poor soil, give poor-shaped stock, and also the reverse. But even with the same kind of good soil used for two seasons, the writer has seen the average tuber shape of a strain change, both in Irish Cobblers and Green Mountains, apparently as the result of seasonal differences in weather condi-

tions. For example, a certain Green Mountain strain, nearly free of the spindle-tuber disease, was planted on sod-land Caribou loam on Aroostook Farm in 1921, at such a time that the early growth was exposed to weather unfavorable enough so that many of the plants began to bud when only a few inches high, and most of the buds dropped off without opening.[3] These unusual weather conditions were followed by good growing weather so that the vines became large and yielded over 150 barrels[4] an acre in spite of the poor start and the removal of 10 per cent of the hills, affected with mosaic and leafroll. However, there was a light set, or small number of tubers per hill, and apparently as a result of this, together with the season's unusual weather, most of the tubers were over-grown or poor-shaped or both. Some of the shapes are shown in Fig. 7, where seven flat, tough-skinned, apparently disease-free tubers of as many different shapes are shown (B-H) in addition to a spindle-tuber potato (A). Two barrels of the best-shaped tubers were selected in the bin and planted separately from the bulk which was all planted on Aroostook Farm. Both the selected and the bulk, which was field-run because all the available seed of this stock was wanted, gave very uniformly shaped tubers in 1922, much in contrast to the crop of 1921. The first part of 1922 was wet, instead of dry as in 1921, there was a heavy set or large number of tubers per hill, and the vines never became large. The yield rate was only between 90 and 100 barrels an acre and the many small tubers were short and flat, not spindle-shaped. The seed-tubers shown in Fig. 7 were planted whole and later in the season before they had decayed (being protected by the uncut skin) they and their progeny were dug. As shown in Fig. 7, the spindle-shaped tuber (A) and the oblong flat tuber (F) produced spindle-tuber hills, which are to be explained in connection with diseases. The others all gave similar healthy hills of small, flat, oblong to round tubers. Thus it is apparent that poor-shaped tubers can have good-shaped

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[3]In the same season, later-planted Green Mountains on a different farm yielded many seed-balls from the blossoms, as high as a dozen to a plant being obtained containing fertile seed. Probably over a quart of seed-balls to an acre could have been obtained, while samples from the same seed-stock early-planted on Aroostook Farm gave no blossoms.

[4]A "barrel" is a barrelful or 2¾ sixty-pound bushels. 150 barrels therefore are about 410 bushels.

progeny if they are disease-free, and that seasonal conditions may affect tuber shape in a strain in good soil, regardless of disease.

The same change from 1921 to 1922 was seen in another stock of Green Mountains. In 1921 there were many dumb-bell shaped tubers and even the growing together of tubers in chains and clumps. In 1922 the shape was satisfactory except for scattered diseased hills, the soil being more fertile than on Aroostook Farm and a higher yield rate and more oblong tubers being obtained.

In the Irish Cobbler variety, two stocks were compared in 1921 in Aroostook County and again in 1922 both in Aroostook County and in a more southern region. In 1921, one stock had large vines, light set, high yield rate, and coarse over-grown tubers, while the other gave a low yield rate but mostly good-shaped tubers. In 1922 the former stock produced a crop satisfactory in both places as to shape and yield, while the latter stock, though from better shaped seed, gave a disappointing crop, showing a high percentage of infection with spindle-tuber and another degeneration disease.

With recognition of the immediate effects of soil and climate upon tuber shape, there remain several other causes of poor tuber shape. The one to be given the most space in this bulletin will be called the "spindle-tuber disease" or "spindle-tuber" in brief. As will be explained later, climate at least, and possibly soil also, may have an indirect effect on tuber shape by influencing the spread of the spindle-tuber disease. In addition, the effects of the spread of spindle-tuber usually are not apparent until in the next season after the spread, and often there is a change of soil or seasonal weather meanwhile. Therefore it is not surprising that the effects of this disease often have been attributed solely to soil and weather. Even when it is noticed that spindle tubers are grouped in hills scattered throughout the field and are therefore not correlated with soil or weather directly, inasmuch as the bad hills have the same general environmental conditions as the good ones, still soil and weather are blamed on account of the opinion that certain soils and climates tend to cause potatoes to "run out" with the effects showing up in the next or following season. The fact that a contagious disease is involved was formerly not suspected. Knowledge of that fact now offers hope of better control of tuber shape.

In addition to the spindle-tuber disease, other diseases such as curly-dwarf and Rhizoctonia disease often produce poor-shaped tubers. Also, in apparently healthy hills, in a good season and in good soil, occasionally tubers can be found very different from the others in shape, being long and narrow, but they are without the abnormal skin, eyes, and ends of spindle tubers.

Causes of Running-out or Degeneration

It has been stated previously in this bulletin that poor tuber shape can be attributed to several causes, one being a spindle-tuber disease. There is another general side to the problem that should be explained before this disease is discussed in detail. Spindle-tuber is a degeneration disease in the same general class with mosaic and leafroll[5]. It was because of experience with mosaic and leafroll that suspicion arose, and evidence was secured easily, that the spindle shape of tubers often might be due to disease. Knowledge of these other degeneration diseases prepares one to understand the spindle-tuber disease better, so that degeneration in general will now be discussed briefly.

Degeneration or running-out may be defined as a more or less continuous change for the worse in a strain or stock in regard to vine growth, yield rate, or tuber shape, or combinations of these qualities. It often progresses more or less steadily until a strain perishes, is discarded, or reaches the low level of a completely diseased condition. Authorities agree that potato degeneration has been going on in Europe for at least 150 years, with the cause probably consisting largely of degeneration diseases.[6] At least it is clear that the degeneration described by earlier writers is like that now known to be caused by contagious troubles. Degeneration diseases, as other kinds, are influenced by climate and soil, but even with the same climate and soil there often is danger to good stock, or hills, from association with degenerate stock, or hills. Degeneration diseases have their

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[5]See Maine Station Bulletins 292 and 297, by the present writer.

[6]Krantz, F. A., and Bisby, G. R. Relation of mosaic to running-out of potatoes in Minnesota. Minnesota Agri. Exp. Sta. Bul. 197, 1921.

Salaman, Redcliffe N. Degeneration of potatos. Rpt. Internat. Potato Confer. Royal Hort. Soc. London 1921, p. 79-91.

causes in the juice[7] of the plants. The causes, being in the juice, remain permanently after their introduction into a plant, perpetuated from one generation to another by the tubers.

It follows from the preceding statements that often, and for a long time, potato strains have been seen to change more or less rapidly for the worse from season to season without its being realized that the basic trouble was one or more maladies that spread from diseased to healthy plants. Usually more or less time elapses, after a degeneration disease is contracted, without any effects being seen, the juice meanwhile perpetuating the disease; consequently the relation of the disease effects to the spreading agents, insects, was not readily perceived. At length tobacco mosaic and spinach mosaic were noticed to increase shortly after waves of aphids (plantlice) spread. This led to experiments which proved that aphids transmitted these diseases. It was then shown that potato mosaic also is spread by aphids; but with the last of the season's growth in the tubers rather than in the leaves, and with mosaic appearing only in the leaves, it was only when aphids spread mosaic very early in the season that the effects were seen in the leaves the same season. However, it was not difficult to prove the spread of potato mosaic by aphids, by keeping the tubers of exposed plants, rows, and stocks separate from the tubers of corresponding ones not exposed to aphids from diseased plants, and by making comparisons the next season. After proving this for potato mosaic, potato leafroll was studied similarly and proved likewise to be spread by aphids.[8] Mosaic and leafroll have conspicuous effects on the foliage and usually no apparent effects on the tubers except for reduction in yield rate. Spindle-tuber has a relatively inconspicuous effect on the foliage and usually a pronounced effect on tuber shape, but is spread and perpetuated in the same ways as are mosaic and leafroll. Therefore it belongs in the same class of diseases and has had to be studied with the same methods, keeping tubers from exposed plants, rows, and stocks separate from others and observing the second generation or progeny.

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[7]"Juice" is here used in a very general way to include both the liquid part of the plant and whatever of its contents are removed by transmitting sucking insects. The actual causes are at present still unknown.

[8]See Maine Station Bulletins 292 and 297, cited previously.

THE SPINDLE-TUBER DISEASE

EFFECTS UPON THE PLANTS, TUBERS, AND YIELD RATE

The Green Mountain variety has been studied most in this connection and will be considered first. Plants that come from tubers showing the disease are different from healthy plants in having more erect and more spindling shoots (see Figs. 9 and 11.) The leaves are smaller, more erect, and early in the season are somewhat darker green with more rugosity, that is, with the leaf surface raised between the veins, thus decreasing the leaf's smoothness and flatness (see Figs. 9 and 10). Later in the season the leaves are even more dwarfed but the rugosity is not so marked (Figs. 10 and 12.) These effects on the vines are not so conspicuous as those of mosaic or leafroll. Quite similar effects are often seen in young, late-sprouting, and single-stalked healthy hills, so that correct and complete detection of the diseased hills scattered throughout a field is difficult. If, however, the seed-pieces from a diseased tuber or hill are all planted consecutively in the row, the contrast with healthy tuber-units or hill-units is usually obvious. The most striking effect of the disease is on the tubers, which are made spindling, long, and cylindrical, with a more irregular or bumpy outline, more spindle-shaped or tapering ends, and more conspicuous eyes (Fig. 13). Usually the skin of a spindle tuber is smoother and more tender, and in the spring the flesh cuts more easily. This sequence of effects, beginning with obviously diseased tubers, is shown as series A across the top of Fig. 5. In this figure the effects of the spindle-tuber disease are represented in the tubers by elongation and in the plants by uprightness of the leaves, shown in an exaggerated degree. The blackening of the diseased tubers is not intended to represent any natural effect of the disease, but only to help distinguish such tubers in the diagram.

The preceding sequence is seen when the seed-tubers show the disease. Seed-tubers also may be healthy in appearance, and yet may be perpetuating the disease in their juice as the result of the parent hills having become infected late in the preceding season (series B in Fig. 5.) In such cases, the plants show the disease as soon as they come up, but generally are not so dwarfed as the plants from spindle tubers. It seems possible that absence of the disease from the parent plants during the first part of the

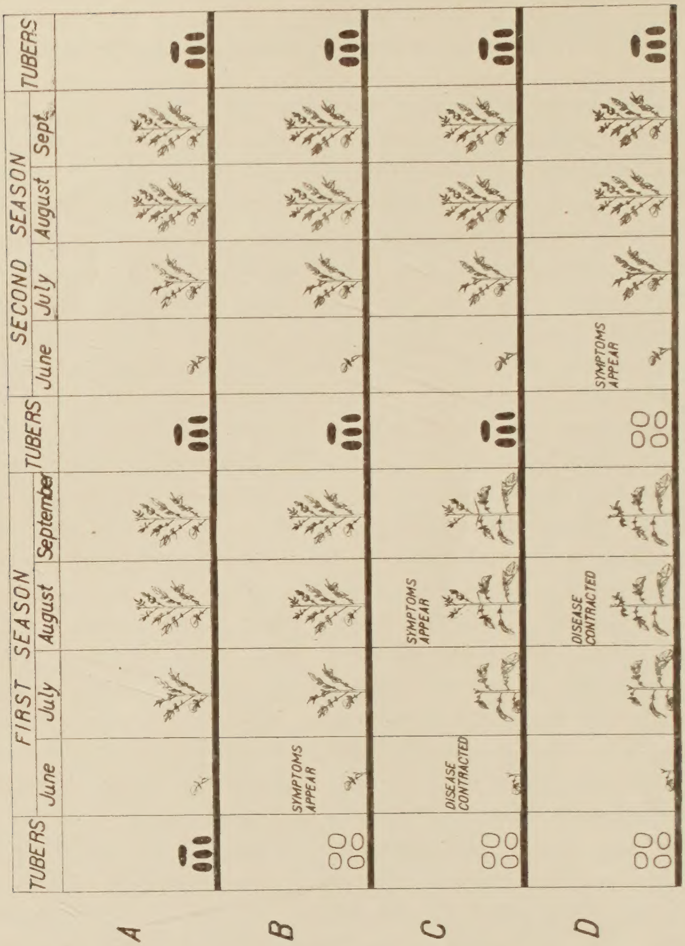

FIG. 5. Diagram representing four series of plants and tubers, all series extending through two growing seasons but each series having the spindle-tuber disease contracted at a different time. For a full explanation see pages 27-29, under "Effects upon the plants, tubers, and yield."

season permits more starch and other food to be stored in the tubers than when the disease is present from the beginning, so that the seed is more vigorous.

Two types of sequences have now been described. The first has the disease showing both in the seed-tubers and in the plants throughout the season and of course also in the tubers. The second has the disease actually in the seed-tubers but not showing there because of the disease having been contracted by the parent vines too late to have any apparent effect on the plants or tubers in that same season. In a third type the plant begins growth from a healthy seed-piece and at first is healthy in appearance and in fact, but disease is introduced early enough to have its effects on the upper, last-formed leaves and upon the tubers. This type of sequence is shown in series C of Fig. 5, where it is indicated that the disease is contracted in June with the first effects appearing in the top of the plant in August, with the tubers then also showing the effects. This condition is seen in certain experiments (H-ST, Figs. 12 and 13) but not in commercial fields in northeastern Maine where spread seems to be effected by insects late in the season. This late spread gives a fourth type of sequence, where the vines and tubers get the disease late and show no effects except in their progeny. Such a sequence is shown in series D of Fig. 5, where it is indicated that the disease is contracted in August of the first season without showing any effects in the plants until the next June, or in the tubers until September of the second season. Series D is like series B except that the disease is contracted a year later.

These are the usual effects in Green Mountains. However, in spindle-tuber hills there sometimes is a small percentage of tubers with the general short, wide shape of healthy tubers, but the skin, eyes, ends, and regularity of outline are still affected. Just as mosaic seems to act differently in different varieties, so the spindle-tuber disease does not have the same effects in all varieties. In soil of at least one type, Caribou loam, the disease in Irish Cobblers and Bliss Triumphs causes a difference in color of the tuber skin, which becomes browner and duller in the former variety, and lighter pink and somewhat blotchy in the latter variety. In addition, the effect on shape is much worse in the Cobblers than in the Triumphs (Fig. 14). In Spaulding Rose 4 (Northern Red or King), the tuber-skin is made lighter in color

by the disease, while the leaves are not changed as much as in Green Mountains (Fig. 8). In Rurals the tuber-skin is made smoother, as in Green Mountains, but the tubers are not changed so much from flat to cylindrical (Fig. 14). Some of these varieties need further study with infection induced experimentally under control from diseased hills of the better understood varieties.

Marginal leafrolling has been reported as a symptom of spindle-tuber in New York[9] and New Jersey[10], and growth cracks in the tubers in New Jersey[10]. The inferior Irish Cobbler stock mentioned on page 24 was reported (by letter) as showing much leafroll in Pennsylvania ,though showing none in northeastern Maine. True leafroll is distinguishable in New Jersey and was plain in northeastern Maine in experimental stocks kept as a leafroll reservoir. Apparently spindle-tuber, like other degeneration diseases, may have somewhat different effects in different regions. Slight rolling is shown in Fig. 12, and some growth cracks in group A of Fig. 7, in Maine Green Mountains.

The apparent effect on the yield rate of individual hills is a marked reduction (Fig. 8). This has not yet been confirmed on a large scale except in two strains where there was also complete infection with mosaic. Three parts of the same strain of Green Mountains were compared in northeastern Maine on Aroostook Farm in 1921. A sixteenth-acre 2-row plot all mosaic and all planted with healthy looking seed yielded at the rate of 96 barrels an acre. This plot was between two other sixteenth-acre 2-row plots, also entirely mosaic but planted with spindle-tuber seed, both of which yielded at the rate of 68 barrels an acre. The difference between 96 barrels and 68 barrels can be attributed to the difference in the health of the seed used, with the reduction due to the spindle-tuber disease. This difference might have been still greater had the healthy looking seed been actually healthy; about a third of it gave spindle-tuber plants. On either side of this group of three plots was an eleventh-acre three-row plot planted with healthy looking seed which, like the 96-barrel plot in the middle, had about a third of the plants spindle-tuber. These two outside plots were different from the 96-barrel plot in having

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[9]Fernow, Karl H. Spindling tuber or marginal leaf-roll. (Abst.) Phytopath. 13:40. 1923.

[10]Martin, Wm. H. Loc. cit.

only a third of the plants mosaic instead of all, and they yielded at the rate of 142 and 150 barrels an acre respectively, averaging 146 barrels. Thus mosaic reduced the yield about the same proportionally, but more absolutely, than the spindle-tuber disease.

In 1922 one commercial, 12-acre diseased field of Green Mountains that the writer had under observation was all mosaic with 80 per cent of the hills also spindle-tuber. It was planted alongside of another comparatively healthy 12-acre field of the same variety with about 20 per cent of the hills spindle-tuber, and mosaic absent in 1921 and less than 5 per cent in 1922. The doubly-diseased stock died down much earlier than the other and was reported as yielding about half as much. The higher-yielding healthy stock had not been used entirely as seed because in 1921 it had many dumb-bell shaped tubers and also tubers growing together in chains and clumps (see p. 24, in connection with weather effects on shape). This illustrates the danger in a strain of the perpetuated spindle-tuber disease and mosaic together as compared with temporary poor shape due to seasonal conditions.

Even if the yield rate were not reduced, and even when its reduction is not realized, there still is cause for complaint about spindle-tuber because of the effect of the disease on the quality of the tubers. The off-type shape is undesirable in table stock because of the tender skin being more easily bruised, because it increases the chances of small tubers of a given weight or volume to slip through grader holes of a given diameter, and because it sometimes makes "long whites" grow in stock to be sold as "round whites." It is even more undesirable in seed stock because it either makes culls or, if not culled out, it detracts from the appearance of varietal purity. When perpetuated in healthy looking tubers it may cause an unexpected and puzzling disappointment to the seed-buyer when he digs his crop, being reported from some other regions as causing reduction in yield[11] and postponement of ripening off and early digging. There is need for much further study of the effects of the disease upon yield both in Maine and in seed-buying states south of Maine.

Spindle-tuber has been under observation on Aroostook Farm for several years, a spindle-tuber plot being grown in 1918 with tubers from a commercial lot. The lack of transportation

[11]Martin, Wm. H. Loc. cit. Yield of primes reduced about 90 per cent, and total yield about 50 per cent.

facilities prevented an adequate potato-disease survey of north-eastern Maine until in 1921. Apparently a number of leading Maine growers who have complained about spindle-tuber effects, especially in Irish Cobblers, have more or less cause for complaint. However, in 1922 a number of fields were practically free from the disease, and there is no apparent reason why healthy stocks can not be rapidly increased providing certain simple, usually neglected precautions are followed (see later section on control measures). Judging by photographs and by various reports from potato growers and scientists, the disease has been observed in a dozen States scattered in the far north-west, the north section, the middle-west, and along the eastern coast, in brief, throughout the potato-growing part of the country. It is depicted in certain scientific bulletins published from 1914 to 1916[12] and probably has been a handicap to the profitableness of potato growing for a number of years.

It may be pointed out here that with diseased hills giving a lower yield than healthy ones in the same field, the percentage of hills that are diseased will be higher than the percentage of harvested crop that appears diseased. Such a discrepancy between the spindle-tuber percentage determined for the hills and that determined for the crop of tubers indicates merely that the diseased hills did not produce as much on the average as the healthy ones, and does not reflect on the accuracy of the field inspection. It may also be pointed out that it is to be expected that the disease will affect the yield rate and the quality differently as the variety, soil, or season is different. Diseased hills in favorable conditions may sometimes out-yield healthy ones in unfavorable conditions. Furthermore, reduction in yield should not be attributed solely to the spindle-tuber disease even when its presence is evident from the appearance of the tubers, unless it is known that there is no other degeneration disease present such as mosaic or leafroll. Sometimes the apparent effect of spindle-tuber disease is due to a combination of this and another disease, like

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[12]Stewart, F. C., and Sirrine, F. A. The spindling-sprout disease of potatoes. New York State (Geneva) Agri. Exp. Sta. Bul. 399. 1915. (See Plate 2.) Stewart, F. C. Observations on some degenerate strains of potatoes. New York State (Geneva) Agri. Exp. Sta. Bul. 422. 1916. (See Plates 1 and 10.) Fitch, C. L. Identification of potato varieties. Iowa State Col. Agri. Ext. Bul. 20. 1914. (See Figs. 2 and 21.)

that described previously with reference to a yield-rate test. On the other hand, mosaic alone may be erroneously blamed for a reduction in yield due partly to unrecognized spindle-tuber disease. Curly-dwarf has effects on the tubers similar to those of the spindle-tuber disease, and there is good preliminary evidence that in Maine, in Green Mountains at least, curly-dwarf usually is a combination of the spindle-tuber disease and one type of mosaic.

PERPETUATION

As is true for degeneration diseases in general, the spindle-tuber disease is perpetuated in the juice of potato plants and tubers after it once has been introduced. This is true even when the disease has been introduced recently and not enough time has elapsed for the appearance of the effects of the disease on vines and tubers. Thus vines that have stopped growth in the late summer, and their tubers that have already got their general shape, may be perpetuating the disease in their juice though apparently not affected.

Another possible place of perpetuation by plants is in weeds. It is well-known that in more southern regions certain degeneration diseases of potato and of other plants are thus perpetuated, sometimes being only in weed roots, underground stems, or seeds during winter. Weeds would not necessarily need tubers to perpetuate the spindle-tuber disease, since *this disease is not a tuber quality, but is an unhealthy condition caused by something in the plant that happens to affect tuber qualities along with vine characteristics.* Perpetuation would depend merely on whether a plant is capable of nourishing the cause of the disease when introduced. At present no weed is known in northeastern Maine which has been demonstrated as a perpetuator.

No tests have been made with the spindle-tuber disease as to the possibility of perpetuation in the soil. Several tests in Maine with other degeneration diseases have shown no soil perpetuation. Earlier tests elsewhere were at first thought to indicate transmission and perpetuation in the soil but that opinion has been changed since aphids, then disregarded, were shown to be carriers. Of course ungathered tubers from diseased plants will perpetuate the disease in a field when they live through the win-

ter, as they do in northeastern Maine in some seasons with an early and continued deep snow covering on the ground. This is the only known way in which a field can perpetuate the disease from one growing season to another, but it is important in regard to the need for planting a seed-plot where there will be no diseased volunteers.

PROOFS OF INFECTIOUSNESS

Statements and references have already been made about juice-perpetuation of the spindle-tuber disease and about its spread from diseased to healthy plants. As explained before (p. 28), these are not often obvious in the field. They must be proved mostly by experiments, but the required experiments are simple and easily performed. Some will be described here.

EFFECTS OF PROXIMITY TO DISEASED PLANTS

When transmitting insects are present, as is apparently the rule in commercial fields, the spread from diseased rows to healthy rows can be proved by sacking separately the samples taken from healthy rows at different distances from diseased rows, and by comparing the next season's crops from these samples. For example, samples taken from the first row of healthy Green Mountain stock adjoining diseased stock on a certain farm in 1921, produced plants in 1922 of which 60 per cent were spindle-tuber. Samples from another row a few yards removed from the diseased stock produced plants with only 10 per cent spindle-tuber. This row-sampling method can be done easily and is recommended to growers who wish to determine for themselves the effects of the season and other conditions on the spread of this disease. In 1922 such sampling was done in a number of fields in Aroostook County, by the writer and others interested in determining when and how far the disease spreads. The chief point of interest in this testing of row-to-row transmission will be explained later in connection with insects.

The spread from diseased hills to healthy ones can be proved by sacking separately different hills of potatoes grown at different distances from diseased hills. For example, healthy Green

Mountain hills taken in 1921 on a certain farm next to diseased hills produced plants of which 30 per cent were spindle-tuber, while other healthy hills from the same field produced no spindle tubers. Here less than one per cent of the hills were spindle-tuber in 1921, and it was easier to get healthy hills considerably removed from diseased ones than where one hill in every five or ten is diseased. In two Irish Cobbler fields in the same year, respectively with 5 and 15 per cent of the hills diseased, a much higher proportion of the healthy hills became infected, as shown by the progeny in 1922. Even here the healthy hills a few feet distant from diseased hills had, in their progeny, a healthy percentage three times as great as that for healthy hills next to diseased hills.

INSECT TRANSMISSION

Aphids (which are juice-sucking insects) have been proved to transmit or spread the spindle-tuber disease.[13] Green Mountain tubers were divided and the parts of each tuber planted under different insect cages. Each of these insect cages, made of a wooden frame with cheesecloth sides and top, kept out aphids unless introduced by the experimenters through the entrance in the top of the cage. After these insects had been transferred from spindle-tuber plants, also grown under cages, to healthy caged hills, the progeny of the latter hills were spindle-tuber. Meanwhile the progeny of the insect-free hills from the same seed-tubers, and the progeny of other sister hills fed upon by aphids from caged hills not spindle-tuber, were healthy. The difference between the different hills, the disease coming only with the aphids from diseased plants, can not be attributed to differences in parentage or environment, since such differences were avoided. Uncaged hills may or may not be visited by aphids in sufficient numbers to transmit the disease, so that they can not be used reliably to prove transmission, even though they may be thought to have become infected. Aphids have been proved to

[13]These insects are more often present and numerous than is generally realized by growers. Their habits are described in Maine Station Bulletins 242 and 303, by Edith M. Patch.

transmit several other degeneration diseases of potatoes, and similar diseases of other plants. They have not yet transmitted spindle-tuber disease early enough for it to appear in the top leaves and in the tubers during the same season as their transference, as has occurred with mosaic and leafroll. Other means of transmission have done so, however.

ARTIFICIAL TRANSMISSION

Certain grafting and leaf-mutilation experiments have supplemented the insect-transmission experiments by showing that juice transfers by other means than juice-sucking insects can transmit the spindle-tuber disease. Tuber-grafts were made by splitting healthy and diseased tubers in two, and in each graft fastening a healthy and diseased half together with the freshly cut surfaces in contact. Ungrafted parts of these tubers were planted in the next row in adjacent hills so that there were both root-contact and vine-contact as in the graft hills, but no cut-surface contact. Eighteen such grafts were made in which the two parts grew plants that at first were respectively diseased and healthy. In these eighteen there were fifteen in which the healthy side became diseased and produced spindle tubers, while the ungrafted healthy mates in the next row, from the same seed-tubers, produced good-shaped tubers (Fig. 13). In brief, tuber grafting infected 83 per cent of the healthy seed-tuber halves early enough for the effects to appear in the same season. No infection occurred in the next row with mere proximity and root-contact of plants grown from other seed-pieces cut from the same diseased and healthy tubers (Figs. 9 and 11).

It is of course probable that in the preceding experiment some of the hills with tubers apparently healthy became diseased during the last part of the season, from insects dispersing in the field, too late to show the effects of the disease. Because of this danger of late-summer insect infection, when artificial transmission was attempted with stem-grafts and leaf-mutilation, necessarily later in the season than was attempted with tuber-grafts, the treated plants were grown inside of insect cages. Stem-grafts were made by fastening a wedge-shaped bud-bearing piece of a young diseased stem, from an insect-free caged plant, between the halves of a split young healthy stem. Leaf-mutilation was performed by bruising the young foliage of a healthy plant and

applying the juice squeezed out of diseased shoots, this juice being soaked up by the bruised leaves. Both methods transmitted the disease early enough for the effects to show in the tubers. The untreated caged sister hills, from the same seed-tubers, remained healthy showing that the disease came from the inoculating treatment and not from the seed-tubers. These various artificial methods have been effective with other degeneration diseases, except that leaf-mutilation has not yet transmitted leafroll, and they give further indication that the spindle-tuber disease is of the same general type.

Careful tests of the possibility of transmission by the seed-cutting knife have not been made. Tubers obviously diseased would be discarded and not cut. To avoid any possible transmission from apparently healthy tubers perpetuating the disease, to actually healthy ones, would necessitate sterilization of the knife after cutting each tuber, an impractical process. Knife transmission if occurring readily would greatly increase the amount of disease in a stock and make other selection measures useless. The writer has seen many tuber-units (groups of sister-hills) from healthy tubers each of which had been cut immediately after cutting a diseased tuber, with no sign of the disease having been introduced into the seed-pieces. A more careful test with mosaic showed no transmission by the knife.

EFFECTS OF VARIATION IN ENVIRONMENTAL CONDITIONS

Effects of various environmental conditions on tuber shape aside from disease have been described in the first part of this bulletin. The influence of the variety on the effects of the disease has also been mentioned. This needs further study so that the disease can be identified more certainly in all varieties. Weather and climate may perhaps modify the effects of the disease when it is present, as with mosaic which is not so plain in certain seasons and places, but this problem has not been studied. As far as is known, soil conditions may possibly modify the signs of disease in the tubers, since they modify the appearance of healthy tubers.

An entirely separate problem is involved in the effect of variation in environmental conditions on the spread of the disease. Weather, season, and climate may have an effect that

probably is mostly indirect, by influencing somewhat the number, distribution, and dispersal of transmitting insects, by determining somewhat the number of perpetuating weeds, if any, and by affecting the length of the growing season of the plants. The number of transmitting insects also may vary rather independently of the weather, depending on the development of their enemies, on the abundance of their food-plants, and on the effectiveness of control measures against them.

It is often stated that northern-grown seed is better than southern-grown. The general truth of this seems to be partly due to a less degree of spread of spindle-tuber and other degeneration diseases. Sometimes southern-grown seed is better than northern-grown when it is grown so as to be more free from such diseases, but to do that is apparently not easy.

It is also often stated that the change of location or the shifting of a strain from one farm to another is in itself beneficial. This may or may not be true. The writer has seen cases of introduction or shifting of seed-stock that, because of more disease being present, resulted in the grower having a worse crop than where he had planted his own seed. The writer also has seen stock do worse in the season after shifting than in the season before, because of an increase of disease or because of unfavorable differences in the weather or soil. Therefore a change of location of seed-stock does not necessarily cause an improvement either in the shifted stock or in the crops of the new grower. When a change is accompanied by improvement in the crop, the benefit is often due to the selection of disease-free stock. Also, with disease not a factor, shifting seed-stock is, according to the laws of chance, as likely to be accompanied by an increase in good growing conditions from one season to another, as to be accompanied by a decrease in good growing conditions. In brief, a grower may expect a *change* to new seed-stock to be a real benefit or not, depending on various conditions. Also, even when a change seems beneficial, the benefit may actually not be due to the fact that the stock is growing on a different farm.

The idea of shifting seed being in itself beneficial, is implied in the common statement that an *exchange* of seed will do good to the stocks of both growers. If the two stocks are different in value, at least one grower may be expected to profit on that account. If the two stocks are alike in value, both growers have

an even chance of improvement from the season being more favorable than the preceding one. Proof of the exchange itself being influential would consist in two growers exchanging seed in part, and *each one* finding that on his own farm his own seed was inferior to that got from the other grower. Accurate comparison on each farm between exchanged and homegrown seed would require more than the usual care taken to determine yields. Proof would not result from one grower benefitting by the exchange, inasmuch as that would be expected unless the two strains were exactly alike. Nor would it result merely from both strains doing better after exchanging than before, with no comparison with the home-grown seed, since both strains even if not shifted might do better in one season than in another because of seasonal differences. Such evidence as would meet these requirements has not become available to the writer. Unless it is available, the emphasis should be laid on the known causes of seed improvement such as greater freedom from disease, and on this and other causes of crop improvement such as the growing conditions provided by climate, soil, and agricultural practices.

CONTROL METHODS

There are two general ways in which control methods must be directed to eliminate or reduce the spindle-tuber disease, or at least to reduce its spread and its increase as much as possible, (1) by selecting tubers, hills, rows, or strains that are not perpetuating the disease and (2) by keeping them separate from those that are perpetuating the disease so that there will be no contamination. Several special control methods will be discussed as to effectiveness.

TUBER SELECTION

There are often three different classes of tubers—(1) actually and obviously diseased, (2) actually healthy, and (3) actually diseased but apparently healthy. The last type exists because of infection of the parent vines late in the season. If no hill-to-hill spread has occurred in the field, of course apparently healthy tubers are actually healthy, but the writer has not yet seen condi-

tions in which there was no hill-to-hill spread except where all the hills were healthy or all were diseased. Such spread has occurred even when there was not what the writer would call an abundance of aphids, indicating either that a few of these insects can accomplish transmission in the field, or that other kinds of insects are sometimes responsible. Regarding the choice between these explanations, on one hand infection of a very young potato plant with mosaic has been effected with a single aphid, and on the other hand other sucking insects of certain types found on potatoes in Maine[14] have been reported elsewhere as transmitting degeneration diseases such as spinach mosaic[15] and potato leaf-roll[16]. In brief, in our present state of knowledge there is no way of learning ahead of time how large a proportion will be diseased in the progeny of apparently healthy tubers from a field containing diseased plants. Five per cent of the hills diseased one year have contaminated as high as 70 per cent of the next year's progeny of good-shaped tubers.

HILL SELECTION

It has been described (p. 34) how hills selected as healthy and not next to diseased hills had a higher proportion of healthy progeny than similar hills selected next to diseased hills. In such cases transmitting insects dispersed and transmitted disease more readily between adjacent hills than between those more distant. This general effect of greater distance is not surprising. The real difficulty, however, is in ascertaining just how far a healthy hill must be away from a diseased hill to be certain, or at least likely, to escape infection. In a field of one variety when less than one per cent of the hills were diseased it was possible to select actually healthy hills without any failure. In a field of another variety, the presence of five per cent made it impossible by hill selection to avoid a considerable increase of the disease in

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[14]Patch, Edith M. Aroostook potato insects. Jour. Econ. Entom. 15:372-373. 1922.

[15]McClintock, J. A., and Smith, Loren B. True nature of spinach-blight and relation of insects to its transmission. Jour. Agr. Res. 14:1-59. 1918. See p. 51.

[16]Murphy, Paul A. Leaf-roll and mosaic, two important diseases of the potato. Jour. Dept. Agri. Tech. Instr. Ireland 22:281-284. See p. 283.

the stock. These two cases are not strictly comparable because of possible difference in varietal susceptibility and in abundance of transmitting insects. More light may be thrown on the subject when the progeny are grown of the numerous samples taken in 1922 from healthy rows at different distances from diseased fields. In brief, the only advice to be given now as to hill selection is to expect better results as the selected hills are more distant from diseased hills and, therefore, as the percentage of hills diseased is smaller.

REMOVAL OF DISEASED HILLS

In machine-planted stock, even with a low disease percentage it probably will be very difficult to detect and remove the scattered spindle-tuber hills before digging time. Removal even at digging time would be practical only on a small scale with the time for digging limited as in Maine. Removal of hills at digging time is only a form of tuber selection, removing the obviously diseased tubers somewhat better than can be done on the rack or in the bin, where some tubers from diseased hills may pass as good-shaped tubers. Hill removal or roguing in machine-planted fields is not advisable considering the work involved and considering that the disease spreads to apparently healthy plants from diseased hills growing in the field all summer, these serving as sources of infection by insect transmission.

The only promise of help from removing diseased hills is given by tuber-unit planting. As stated previously in this bulletin, when the seed-pieces from a diseased tuber are all planted consecutively in the row, the contrast with similar healthy tuber-units is usually obvious. This method of planting was performed in part of the seed-plot on Aroostook Farm in 1922. As a result it was possible to remove, early in the season, all tuber-units that were wholly or mostly diseased. However, a few tuber-units contained one or two diseased hills apiece, as is often seen with other degeneration diseases, so that the diseased hills were not eliminated entirely. Observation of the progeny and further tests of the method are required.

INSECT ELIMINATION

Tuber selection, hill selection, and the removal of diseased hills at the end of the season on the basis of tuber shape, should

be very effective control methods providing all transmitting insects are eliminated. However, at present the transmitting power of some kinds of prevalent potato insects has not yet been tested adequately. Further, the methods tried so far against aphids, the only proved insect transmitters of the disease, have not eliminated them. The usefulness of some methods that reduced aphids in 1922 will be judged by the amount of disease in the progeny, and further study is needed. At present it seems that insect elimination in partly diseased stock is not as advisable, considering the cost, as the securing and isolation of new healthy stock.

ISOLATION

It is useless to consider isolation unless fewer than five per cent of the hills are diseased. As stated before, with five per cent diseased there has been enough spread from hill to hill to raise the percentage to 70 per cent in the progeny. A little analysis with reference to Fig. 6 will show the reason. When the percentage of hills diseased is respectively 1, 3, 7, and 30 per cent, the number of healthy hills a few feet distant from diseased hills is progressively smaller. If the hills are about a foot apart in the row, the rows at 3-foot intervals, and the diseased hills scattered uniformly so that each one is equidistant from the six nearest ones, then at these four percentages the greatest distance that healthy hills can be separated from diseased is respectively 7, 3.3, 1.5, and 0 feet, when each hill has a diameter of two feet, or foliage spread of one foot each way. These specifications approach conditions in commercial fields. Therefore each hill will be much more exposed by proximity to diseased hills when the latter are 7 or 3 per cent of the total than when they are only 1 per cent. Perhaps the limit should be below 3 per cent for consideration as to isolation. This limit of course concerns any one disease; an all-mosaic field may be free from spindle-tuber and isolated from spindle-tuber stocks.

Up to 1921 inclusive, not more than a dozen commercial fields of susceptible varieties had been observed with a small enough percentage of degenerate hills to permit testing the effect of isolation. A study of several of these showed that mosaic spread over a gap of 90 feet, but not always over 150 feet. The

others, though with a small disease percentage, unfortunately were not isolated, and a study of these indicated that probably at least ten rows should be discarded next to adjacent diseased stock if healthy stock is to be kept healthy. In 1922 a few sam-

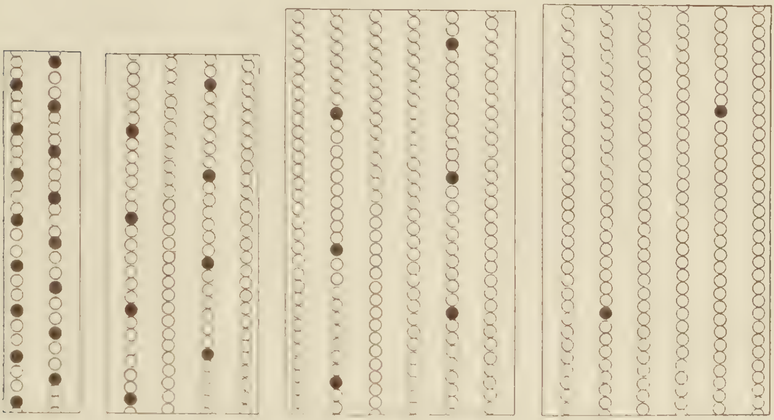

FIG. 6. Diagrams for the comparison of stocks with respectively about 30, 7, 3, and 1 per cent of the hills diseased. Each diagram represents a unit area of the field, that is, in order to represent the whole field with diseased hills arranged as indicated, it is necessary merely to duplicate the diagram and adjoin the duplicates in the same position. The diagrams represent the hills (circles) with centers averaging a foot apart and the rows with middle lines three feet apart. The diseased hills (black circles) are scattered uniformly so that each one is equidistant from the six nearest ones in the field (though not in the unit areas shown here). Note the greater proximity of healthy to diseased hills with the increase in disease percentage. Such proximity is considerably greater with 3 per cent than with 1 per cent, even though both percentages are small, and causes a corresponding greater exposure to infection from diseased hills.

ples were taken to test the effects of isolation and many were taken to test the effects of proximity to disease. The results will appear in the progeny in 1923.

The writer has seen fields of several strains, in several varieties, each with less than 5 per cent (some with less than 1 per cent) of hills degenerate. Some were Maine-grown and others had been brought into the State. Isolation of such healthy stock has in some cases been great enough to keep it disease-free. The securing and isolation of disease-free stock is recom-

mended in preference to any other control method. If, through misunderstanding, a grower's healthy stock has been planted adjacent to diseased stock, it is better to discard the more contaminated part of the originally healthy stock than to mix it up with the remainder causing a high percentage of diseased hills the second year scattered through the stock. In replacing his own stock by a new strain, a grower may be concerned with the question of differences in inherent vigor between strains of the same variety. At present the writer knows of no such difference that could not be due to difference in disease or in conditions of production or storage of the seed-tubers. An accurate comparison of supposed different strains of the same variety should include, among other things, assurance that the origin and variety are really identical, growth and storage of the seed-tubers in the same conditions(same farm and storage-house), complete freedom from disease, and similar conditions of growth (alternating plots). Until such a test is made the question is open as to whether one disease-free strain of a given variety is as good as another for continuous growth on his own farm.

When considering the securing and isolation of disease-free stocks, several things should be kept in mind. Stock may not be disease-free the next year if not already isolated this year. Seed planted where diseased tubers survive in the soil will not be isolated. Diseased stock is as dangerous on the neighbor's land, if near-by, as on one's own land. The least distance needed for isolation is not known but probably varies with conditions of weather, climate, amount of disease in the nearest field, and the abundance and kinds of transmitting insects there. In general, the more isolation, the better the results to be expected.

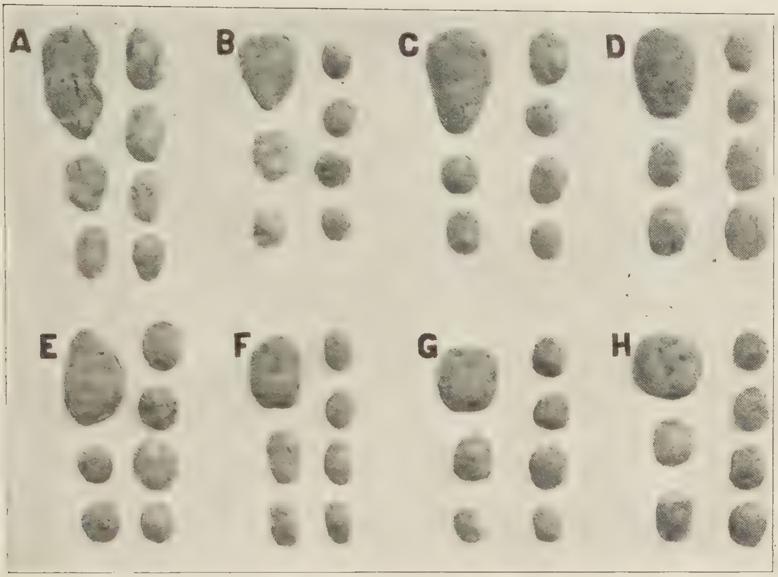

Fig. 7. Shape in Green Mountain seed-tubers and in their progeny. The large tubers A to H were grown in the same field in 1921, were selected from the same barrelful, and were planted whole on June 26, 1922, in northeastern Maine. On September 2 they were still undecayed, and were dug up along with the tubers of their progeny and photographed with their respective progeny as shown here. Tuber A was obviously spindle-tuber, as were its progeny, shown with it. Tuber F was apparently healthy, but its spindle-tuber progeny showed that it had come from a plant that contracted the disease late in the summer of 1921. The six other tubers, although differing in shape, were flat and apparently healthy, and their progeny were not spindle-tuber.

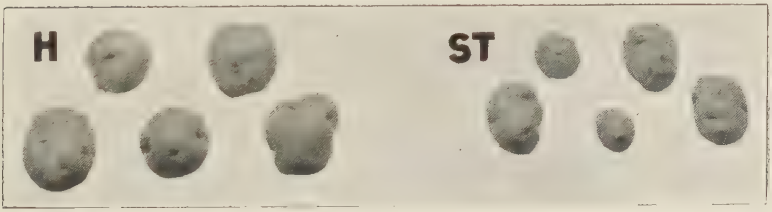

Fig. 8. Tubers of two Spaulding Rose 4 (Northern Red or King) hills, respectively healthy (H) and spindle-tuber (ST). Photographed September 17, 1922, in northeastern Maine.

FIG. 9. Young hills of the Green Mountain variety, spindle-tuber on the left and healthy on the right. Note in the healthy hill the less upright habit of leaf growth and the smoothness and flatness of the leaf surface. Photographed in northeastern Maine on July 6, 1922. See Fig. 10 for details of leaves.

FIG. 10. Leaves from corresponding parts of the Green Mountain hills of Fig. 9, photographed on the same date. Note that the surface of the diseased leaf (ST) is more rugose (less flat and smooth) than the healthy leaf (H).

FIG. 11. Parts of the Green Mountain hills of Fig. 9 photographed about eight weeks later, on August 29. Note that the healthy hill (on right) is not so tall as the other and that its upper leaves are flatter and not so small and numerous.

FIG. 12. Upper leaves from corresponding parts of three Green Mountain hills. Leaf ST, from spindle-tuber hill; leaf H, from healthy hill; leaf H-ST, from hill that was a sister hill to the healthy one, i.e., from the same seed-tuber, and that was originally healthy, but that contracted the spindle-tuber disease, through tuber-grafting, early enough to show the effects in the leaves. Photographed August 29, 1922. See Fig. 13 for the tubers.

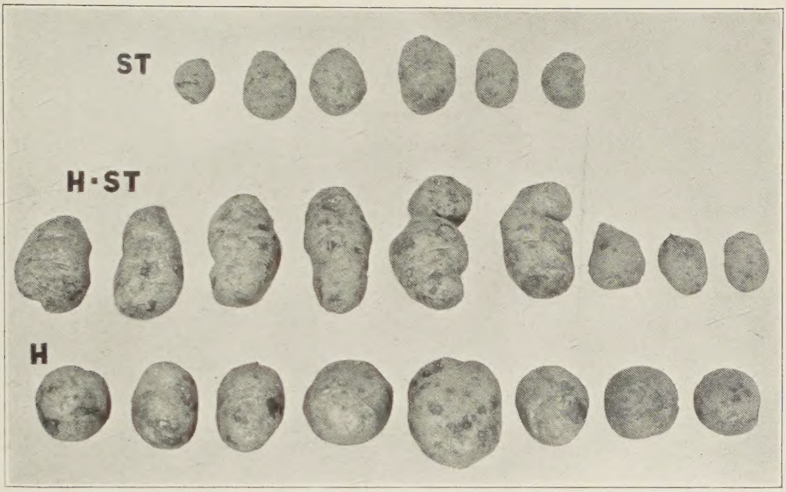

Fig. 13. Three rows of tubers from three hills respectively. Row ST from spindle-tuber hill; row H from healthy hill; row H-ST from hill that was a sister hill to the healthy one, i.e., from the same seed-tuber, and that was originally healthy, but that contracted the spindle-tuber disease, through tuber-grafting, early enough to show the effects in the tubers. Photographed September 1, 1922. The healthy hill grew from a quarter of a tuber and each of the others grew from a half of a tuber. See Fig. 12 for the leaves.

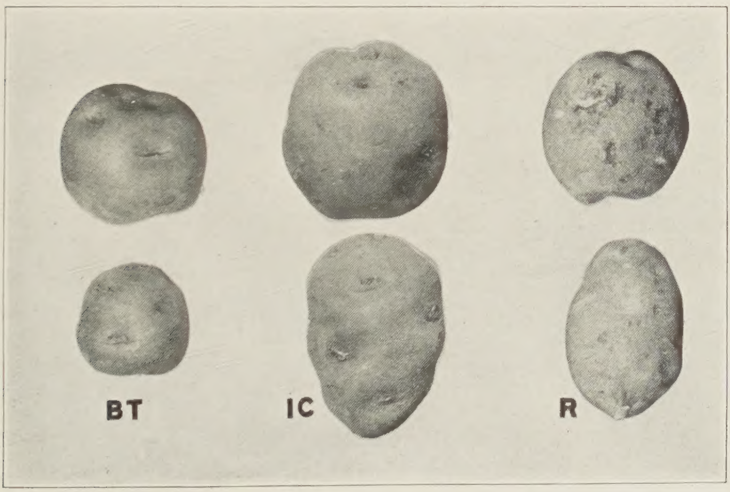

Fig. 14. Spindle tubers below, with healthy tubers of the same varieties above. BT, Bliss Triumph, IC, Irish Cobbler, and R, Rural. Irish Cobblers photographed May 22, 1922, and the others August 29, 1922, in northeastern Maine. See Fig. 13 for Green Mountains, and Fig. 8 for Spaulding Rose 4.